Termite activity and decomposition are influenced by digging mammal reintroductions along an aridity gradient

Coggan, Nicole V.; Hayward, Matthew; Gibb, Heloise

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Termite activity and decomposition are influenced by digging mammal reintroductions

Nicole V. Coggan [1*], Matthew W. Hayward [2], Heloise Gibb [1]

[1]Department of Zoology, School of Life Sciences, La Trobe University, Melbourne, Vic., 3086, Australia.

[2]Australian Wildlife Conservancy, PO Box 8070, Subiaco East, W.A., 6008, Australia.

[2]Current address: School of the Environment, Bangor University, LL572UW, United Kingdom.

*Corresponding author: Email: n.coggan@latrobe.edu.au

Abstract

~~The decline of species~~ Species declines can have broader impacts on ecosystems, particularly when those species act as ecosystem engineers. Ecosystem engineers modify habitats and therefore indirectly shape plant and animal communities. However, environmental attributes, such as aridity, may influence the direct effect of engineers on habitat properties, indirectly affecting other species and the functions they perform. We used three sites where endangered digging mammals had been reintroduced to test the hypotheses that: 1. digging mammal reintroductions affect resource consumption and abandonment by termites, and 2. locality attributes, such as aridity, influence~~s~~ termite interactions with reintroduced mammals. We performed two manipulative experiments to test these hypotheses. First, we tested the effects of ~~burial resource~~ depth on termite consumption of resources (toilet rolls). ~~Here, resource depth was a proxy for disturbance intensity by reintroduced mammals, with shallow rolls expected to experience more disturbance.~~ Second, we tested resource abandonment by termites in response to simulated disturbances by determining the proportion of termites remaining at disturbed resources relative to undisturbed controls over time. Both experiments were conducted at all three ~~aridity levels~~sites, inside and outside exotic predator and exotic digging mammal-free reserves. We discovered that: 1. resource consumption was ~25% lower~~,~~ and resource abandonment ~50% higher where digging mammals were reintroduced; and 2. termite responses to ~~reintroduced digging mammals~~mammal reintroduction became less pronounced potentially ~~-~~as aridity increased. ~~We thus showed that the~~The near-extinction of digging mammals from much of Australia is likely to have significantly altered termite ~~behaviour and termite driven~~activity and decomposition, but that impacts ~~may~~ potentially depend on aridity. Our work should also be considered in the context of reserve carrying capacities as it suggests, counterintuitively, that ecosystem impacts of reintroductions may be lower in resource-poor sites.

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Keywords: Climatic gradient, Critical weight range mammal, Decomposition, Ecosystem engineer, Interactions, Termite

1. Introduction

Recent declines in biodiversity have been dramatic (e.g. Colwell et al., 2012; Dunn et al., 2009), resulting in significant changes to ecosystem functioning and species assemblages (Boyer and Jetz, 2014; Brodie et al., 2014; Feer and Boissier, 2015; Silvey et al., 2015). Australia has the fourth- highest record of species loss (IUCN 2015) and the highest rate of terrestrial mammal extinctions worldwide. Thirty terrestrial mammal species have been declared extinct since European settlement (from 1788). A and a further 21 native mammals are threatened with extinction (Fleming et al., 2014; Woinarski et al., 2015). Non-native predators are amongst the leading contributors to Australia's mammal extinction record (Woinarski et al., 2015). Some of the greatest impacts have occurred in arid and semi-arid habitats, where species of intermediate body size (35 g – 5500 g, referred to as 'Critical Weight Range' species), (McKenzie et al., 2007), and greater mass (up to 10 kg, i.e. Hanna and Cardillo, 2014), have been more susceptible to regional extinctions or declines. The scale of these species losses has been mitigated through mammal reintroductions into fenced reserves, from which exotic predators and other non-native species have been removed (e.g. Hayward and Kerley, 2009; Short and Turner, 2000).

Digging mammals in the critical weight range were almost completely extirpated from Australia's mainland, where arid and semi-arid habitats comprise up to 70 % of the total terrestrial landscape (James et al., 1995). Desertification is increasing globally (Reynolds et al., 2007), *ergo*, the cover of arid and semi-arid habitats is likely to increase in the near future. Australia's native digging mammals are thought to have functioned as ecosystem engineers (sensu Jones et al., 1996). Engineering impacts are generally expected to benefit biotic communities as abiotic stressors increase ~~by providing physiological~~

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~~or physical refuge~~ (Crain and Bertness, 2006). ~~Engineering effects~~ However, their inputs are not adversity. The magnitude of an engineer species' impacts can be context-dependent upon factors including aridity or productivity (hence, resource availability), both of which are important features of arid environments (Fischer and Turner, 1978; Hadley and Szarek, 1981).

Prior to their declines from arid habitats, burrowing bettongs (*Bettongia lesueur*) and greater bilbies (*Macrotis lagotis*) were native digging mammals that made prolific contributions to soil turnover, moving between one to six tonnes of soil per hectare every year (Eldridge and James, 2009). The survival record of these species on the Australian mainland since 1788 is mixed. Bilbies persist in isolated populations in north-western Australia and north-central Queensland (e.g. Southgate and Carthew, 2006) but were lost from their central, south and south-eastern Australian range from the 1910s to the 1930s (Pavey, 2006). In contrast, bettongs became regionally extinct from mainland habitats by the 1960s (e.g. Short and Turner, 2000). Critical weight range mammal declines (especially of digging mammals) represent a broad-scale loss of ecosystem function, with quantified impacts upon the current structure of arid habitats and the biota within them (Fleming et al., 2014; Manning et al., 2015). These include impacts upon multiple aspects of soil (Clarke et al., 2015; Eldridge et al., 2015), invertebrate (Davidson and Lightfoot, 2007; Read et al., 2008; Silvey et al., 2015), ~~and~~ plant assemblages (e.g. Chapman, 2016; Fleming et al., 2014; Verdon et al. in review) and fire regimes (). Re-establishing native mammal assemblages is anticipated to restore impacted natural ecological processes (James and Eldridge, 2007; James et al., 2009; Manning et al., 2015). Digging mammals have been successfully established inside sanctuaries in arid and semi-arid habitats (), but the scarcity of accurate historical data needed for these types of conservation projects means that little is known of their potential interactions with, nor their impacts upon pre-existing ecological assemblages (e.g. Nogués-Bravo et al., 2016).

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Termites are the dominant invertebrate soil engineers and detritivores in Australian arid systems (Morton et al., 2011), and are vitally important to soil health wherever they occur (de Bruyn and Conacher, 1990). Prior to European colonisation, native digging mammals were likely to have been important disturbance agents and predators of subterranean termites and other ground-dwelling invertebrates (Gibb, 2012a; Silvey et al., 2015). Termite activity is sensitive to disturbances ~~which~~that affect the availability and suitability of their resources (e.g. Jones et al., 2003). They are therefore likely to respond indirectly to soil disturbance when mammals are foraging or burrowing (Gibb, 2012a). This may have cascading influences on factors such as habitat productivity, given their input into the functioning of arid systems. In addition to their functional significance, termites are consumed by a variety of fauna (e.g. Colli et al., 2006; Morton and James, 1988; Sheppe, 1970). They are directly relevant to reintroduced digging mammals as one of their primary food sources, as a number of these and other threatened critical weight range species are opportunistic dietary generalists and/or insectivores (e.g. Bice and Moseby, 2008).

Understanding the responses of ecological assemblages to the reintroduction of regionally extinct species is a developing field in ecology. New evidence indicates that critical weight range mammal reintroductions (digging mammals included) have had significant influences on the community assembly of arthropods by initiating trophic cascades (Silvey et al., 2015), and on soil microbes through digging and defecation (Clarke et al., 2015). However, no previous studies have investigated the effects of digging mammals on invertebrate activity and its implication for functions such as detritivory. Understanding the impacts of mammal reintroduction on termite activity is important because of the significant contribution of termites to food webs and ecological processes (i.e. Bice and Moseby, 2008; Colli et al., 2006; Matthews, 1976; Morton et al., 2011; Morton and James, 1988; Sheppe, 1970), particularly in arid habitats (Whitford and Kay, 1999).

We used replicated comparisons of three reintroduction sanctuaries located in arid/semi-arid southern Australia. Our aim was to quantify the responses of subterranean termite activity inside sanctuaries where native digging mammals have been reintroduced, against controls outside the sanctuaries~~,~~ where native digging mammals are regionally extinct. We did this by comparing the proportion of a) resources eaten by termites at different depths, and b) termites remaining at experimentally-disturbed resources buried at both reintroduction and control habitats. We hypothesised that soil disturbances generated by reintroduced digging mammals would reduce termite activity, resulting in lower proportions of buried resources consumed, and higher proportions of resource abandonment by termites. Because aridity was one of the major abiotic variables to increase across the sanctuaries, and also because engineering impacts tend to be context-dependent (Crain and Bertness, 2006; McAfee et al., 2015), we also considered whether different aridity levels at each sanctuary could affect the magnitude of termite responses when digging mammals were present. We hypothesised that the effect of digging mammals on termite foraging would be influenced by the level of aridity experienced at each sanctuary.

2. Methods

2.1. Study sites

We compared termite responses to soil disturbance by reintroduced digging mammals at three conservation sanctuaries. These were Arid Recovery (-30°33’55.38’’S, 136°55’3.85’’E, South Australia), Scotia (-33°8’9.00’’S, 145°11’33.00’’E, New South Wales), and Yookamurra sanctuaries (-34°31’19.38’’S, 139°28’31.91’’E, South Australia) (Table 1, Fig. 1a). Scotia and Yookamurra sanctuaries were administered by the Australian Wildlife Conservancy, and Arid Recovery by BHP Billiton. Aridity varied across sanctuaries. The three sanctuaries were located along a gradient of aridity (Table 1). Temperature, precipitation, gross primary production (GPP) and the enhanced vegetation index (EVI) co-varied with aridity. We used aridity indices for each site that were provided by the Australian Virtual Herbarium (Australian Virtual Herbarium 2015). We placed the aridity index value for each sanctuary relative to the others according to the United Nations Food and Agriculture Organization’s (FAO) aridity index scale. Aridity indices are calculated as the annual mean ratio of precipitation/potential evapotranspiration (Chiew, Wang, McConachy, James, Wright and deHoedt 2002, Tabari and Aghajanloo 2013). ‘High’ aridity indices closer to 1 are less arid than ‘low’ indices closer to 0. Thus, Hyper-arid zones have indices <0.05, Arid zones are <0.05 - <0.20, and Semi-arid zones are <0.20 - <0.50 (FAO 2015). Arid Recovery was the most arid sanctuary and Yookamurra sanctuary was the least arid. Aridity indices, annual precipitation, GPP and EVI increased by an average interval of 34.11%, and the mean daily maximum temperature decreased by an interval of 7.25% from Arid Recovery to Yookamurra sanctuary (Table 1). Note: Aridity indices are calculated as the annual mean ratio of precipitation/potential evapotranspiration (Chiew et al., 2002; Tabari and Aghajanloo, 2013). ‘High’ aridity indices closer to 1 are less arid than ‘low’ indices closer to 0. Thus, Hyper-arid zones have indices <0.05, Arid zones are <0.05- <0.20, and Semi-arid zones are <0.20 - <0.50 (FAO,

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2015). ~~Previous research suggests that effects of (invertebrate) ecosystem engineers on vegetation communities increase with precipitation , and resource scarcity promotes fidelity for termites (Lenz, Kard, Evans, Mauldin, Etheridge and Abbey 2009). We therefore hypothesised that termite responses to reintroduced mammal disturbance would increase with decreasing aridity.~~

The dominant vegetation class for Scotia and Yookamurra sanctuaries was remnant Mallee woodland and shrublands, with climate at Yookamurra classified as 'Mediterranean', while that at Scotia was 'Semi-arid'. Dominant ground cover at Scotia included spinifex (*Triodia spp.*) and chenopod species, and *Westringia rigida* at Yookamurra sanctuary. The dominant trees in Mallee woodlands and shrublands are *Eucalyptus* species, including *E. dumosa and E. gracilis.* Arid ~~recovery~~ Recovery was classified as Acacia shrubland with a 'Desert' climate. Dominant ground cover at Arid Recovery varied with season: at the time of data collection, the Poached-egg daisy (*Polycalymma stuartii*) and Desert Rattle-pod (*Crotalaria eremaea*) were abundant. Sandhill wattle (*Acacia ligulata)* was the dominant shrub species at Arid Recovery. Scotia and Yookamurra sanctuaries supported cryptogamic crust which bound the soil surface at those sanctuaries, whereas Arid Recovery did not.

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2.1.2. Sampling design

All sanctuaries included large (up to ~ ~~86~~000 ha) enclosures free of introduced predators and protected by predator-proof fencing. Reconstruction of native mammal assemblages commenced at Scotia Sanctuary circa 2004 (Finlayson et al., 2008), at Arid Recovery circa 2000 (Moseby et al., 2003), and at Yookamurra Sanctuary circa 1999 (Vieira et al., 2007). All sanctuaries functioned as pastoral land for livestock (sheep and/or cattle) after European settlement and prior to their conversion into sanctuary habitats (Grolleau and Peterson, 2012). All reintroduced mammal species were considered regionally

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extinct from both reintroduction and control areas prior to the establishment of these sanctuaries (Table 1). -Rabbits were present at control habitats, but had been eliminated from inside reintroduction enclosures. The population densities of exotic species in control habitats (e.g. cats, foxes and rabbits) are routinely controlled by sanctuary management using poison baiting, trapping and shooting.

To test the effects of native digging mammals on termite ~~foraging along the climatic gradient~~activity, we performed experiments inside (reintroduced ~~mammalian engineers~~digging mammals present: 'Reintroduction') and outside the reintroduction enclosure (controls with no native ~~mammalian engineers~~digging mammals: 'Control') at each sanctuary (Fig. 1b). We paired sampling sites (n = 6) inside and outside the reintroduction enclosure at each sanctuary. Sites were paired to minimise the influence of spatial autocorrelation of biotic and abiotic characteristics on our response variables. Sampling sites were placed at least 150 m from the fence line (i.e., paired sites were at least 300 m apart) and, where possible, the distance between sites was 1 km (Fig. 1b).

2.1.3. Reintroduced ~~mammalian engineer species~~mammals ~~and presence of reintroduced termitivores~~

We focused on soil disturbances caused by two reintroduced digging mammal species, burrowing bettongs, *Bettongia lesueur*, and greater bilbies, *Macrotis lagotis* (Table 1). These species were important ecosystem engineers prior to their regional extinction from the Australian mainland (James and Eldridge 2007). Bettongs and bilbies are omnivorous and include termites in their diet, although bettongs tend to consume more plant material, while bilbies are more insectivorous (Gibson, 2001; Navnith et al., 2009; Robley et al., 2001). Both species move substantial amounts of soil, within the range of 1.27-5.99 $t.ha^{-1}$ per year (Eldridge and James, 2009), suggesting that termites experience markedly greater levels of soil disturbance inside sanctuaries. Numbats (*Myrmecobius fasciatus*) were

also reintroduced at Scotia and Yookamurra sanctuaries (Vieira et al., 2007). ~~Although this species is not considered an ecosystem engineer, it is exclusively termitivorous.~~ Numbats are exclusively termitivorous (Calaby, 1960), but are not digging mammals and do not function as ecosystem engineers (Table 1). Interactions with numbats were not included in our hypotheses, but were acknowledged as a potential influence on termite behaviour.

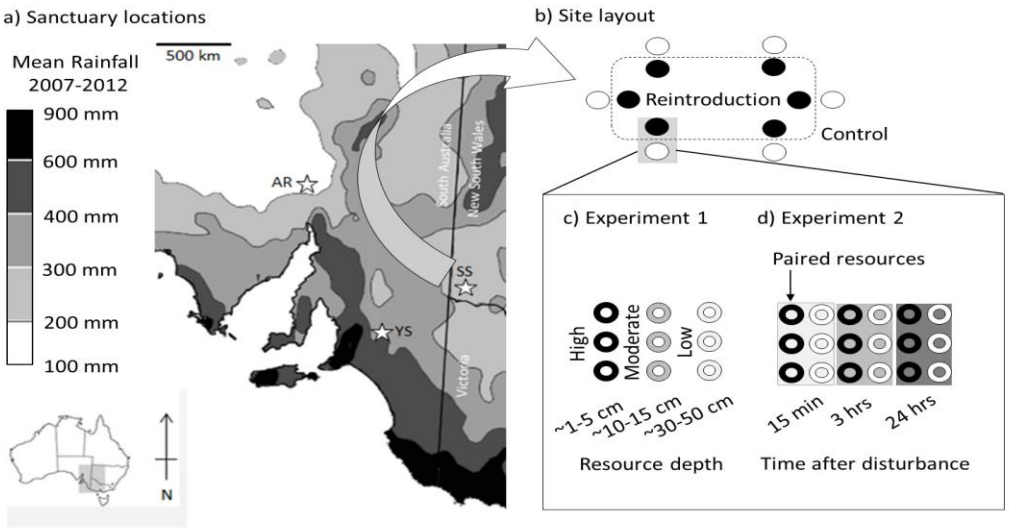

Fig.1 a) Map showing location of study sanctuaries ~~relative to the precipitation gradient~~; b) Simplified diagram of sampling sites at each sanctuary. Dashed line represents the fence dividing habitats. Comparisons of termite responses ~~to reintroduced~~to ~~engineers~~ digging mammals were made between habitats where digging mammals were reintroduced (Reintroduction: closed circles), or regionally extinct (Control: open circles); c) Resource (toilet roll) layout for Experiment 1 showing resource depth ~~(disturbance level)~~; d), Resource layout for Experiment 2, showing 'disturbed' (black) and 'control' (white) resources and layout of blocks by observation time (shaded rectangles). AR: Arid Recovery, SS: Scotia Sanctuary, YS: Yookamurra Sanctuary.

2.1.4. Vegetation Surveys

We performed vegetation surveys in September 2011, prior to commencing experiments. We established twelve 5 m x 5 m quadrats at each of the six paired sites in each sanctuary. In every quadrat, we estimated the percentage cover of four habitat characteristics: bare ground, ground cover, leaf litter and canopy. We also calculated the average volume of logs (lying dead wood) with a diameter ≥ 5 cm in every quadrat (c.f. Gibb and Cunningham, 2010). Standing stems were not measured. Log volume was estimated as the volume of a cylinder in cubic centimetres, using log length and diameter measured at the mid-point of the log. Vegetation cover was predicted to decrease with increasing aridity because precipitation restricts resource availability (Oksanen et al., 1981). It was also expected to decrease where ~~ecosystem engineers~~digging mammals were present, because persistent soil disturbance limits opportunities of for plants to establish (e.g. Gurney et al., 2015). Climate was expected to regulate the impact of digging mammals on vegetation cover in more-arid habitats by limiting the amount of vegetation available for manipulation ~~by engineers~~.

2.2. Termite responses

2.2.1. Experiment 1: Resource consumption ~~under increasing soil disturbance intensity~~.

We performed an experiment using resources buried at three depths to test the effect of soil disturbance by reintroduced ~~ecosystem engineers~~digging mammals on termite ~~foraging across the climatic gradient~~activity. ~~We used resource depth as a surrogate for disturbance intensity.~~ A longitudinal study of soil disturbance indicated that the average foraging pit constructed by bilbies and bettongs is 10-20 cm (Travers, 2013). We therefore expected that resource consumption by termites would be affected most by ~~reintroduced ecosystem engineers~~soil

disturbance at depths less than 10 cm, moderately affected at depths less than 20 cm and not affected at depths greater than 20 cm.

In February 2012, we buried nine unscented toilet paper rolls ('resources') in a 3 m x 3 m grid at each of the 6 paired sampling sites in each sanctuary (Fig.1a-c). We used toilet rolls as resources because they were attractive to common soil and wood-feeding termite genera (*Coptotermes*, and *Heterotermes*), whose ranges intersected all of our study sites (French and Robinson, 1981; Watson and Abbey, 1993). A row of three resources was buried at each of the three depths~~,~~ ~~where depth was a surrogate for disturbance~~. Treatments were: 1) intensely disturbed resources ('High disturbance'), 1-5 cm below ground (these represented the zone of highest resource exposure to soil disturbance); moderately disturbed resources ('Moderate disturbance'), 10-15 cm below ground (these were close to the average maximum depth of ~~engineer~~ diggings); and least disturbed resources ('Low disturbance'), 30-50 cm below ground, where the majority of ~~engineer disturbance~~diggings should be avoided (Fig. 1c). In August/September 2012, we unearthed the resources and visually estimated the proportion of each resource that termites had consumed: 0% consumption indicated that the resource remained intact, and 100% consumption indicated that the resource was completely consumed.

2.2.2. Experiment 2. ~~Effect of intense soil disturbance on resource abandonment by termites~~Resource abandonment.

We hypothesised that disturbance would ~~increase the rate of~~affect resource abandonment by termites. Disturbance caused by reintroduced digging mammals was expected to expose termite foragers to threats such as desiccation or to attack by termite predators, which also include the reintroduced mammals themselves (Table 1). We tested the effects of disturbance ~~on termites~~ by

comparing termite abundances on experimentally disturbed resources with those on controls (undisturbed resources) over 24 hours (Fig. 1d).

In February 2012, we buried nine resources in pairs within a 3 m x 3 m grid at each of the six paired sites at each sanctuary (Fig. 1d). Resources were buried approximately 5 cm below ground, within the range of highest soil disturbance intensity by reintroduced mammals (see Experiment 1). Resource pairs were separated by 5-10 cm and rows were 1 -2 m apart (Fig. 1d). Termites were allowed to colonize resources until August/September 2012, when we applied our disturbance treatment. For each pair, we disturbed one resource by unearthing it and leaving it unburied in its hole, and one resource, the 'control', undisturbed. The purpose of the control resource was to estimate the number of termites using undisturbed resources. We disturbed termite resources between 0900h-1000h to standardize temporal conditions at our sampling sites. Resource abandonment in response to our disturbance was measured by comparing the number of termites in the 'disturbed' and 'control' resources. We examined each row separately at 15 minutes, 3 hours and 24 hours after our initial disturbance treatment. Each replicate resource was examined only once, i.e. termites inside resources from row 1 were collected and counted after 15 minutes, from row 2 after 3 hours, and from row 3 after 24 hours following resource disturbance. For each pair, we counted the number of termites remaining in the disturbed resource and its control. For tests of the effect of digging mammals ~~and climate~~ on resource abandonment, we standardised each response by the total number of termites at the pair (Control-Disturbed)/(Control+Disturbed). We identified termite species whenever soldiers were found (soldiers were required for identification). We also noted predation by ants on termites, i.e., ants carrying termites away ~~(Fig. 1d),~~ at the disturbed resources. Finally, we calculated the proportion of disturbed resources that were attended by ants and photographed ants for later identification to genus.

2.3. **Data Analysis**

We used a generalized linear model (GLM) and Tukey's post-hoc tests with Bonferroni corrections to test the effect of ~~ecosystem engineer~~digging mammal reintroduction on vegetation cover. We also used GLMs to compare termite and ant responses to soil disturbance in habitats with and without reintroduced digging mammals. We used the Gaussian response distribution for termite activity in both experiments. In experiment 2, note that we used the binomial distribution for ant data, as these described either the presence or absence of ants. Tukey's post-hoc tests with Bonferroni corrections were used to determine differences among interacting factors. All analyses were conducted using R (R Core Team, 2015).

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3. Results

3.1. General

3.1.1.Habitat Surveys

Habitat cover differed among sanctuaries, with habitat structure decreasing ~~with aridity~~from Yookamurra to Arid Recovery, and Scotia intermediate between the two (Table 2). Yookamurra had the greatest volume of logs ~~.~~ m^{-2}, the densest canopy, and the least bare ground (Table 2 Post-hoc). At the opposite end of the scale, Arid Recovery consistently had the lowest percentage cover of all recorded habitat types, and had very few logs with a diameter >5 cm, with wood resources concentrated at patches of dead Sandhill wattle (Table 2, Post-hoc). Scotia was similar to Arid Recovery in terms of bare ground and canopy cover, but closer to Yookamurra in terms of ground cover. Leaf litter and logs at Scotia were intermediate between Arid Recovery and Yookamurra sanctuaries (Table 2).

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3.1.2. Termites

Species of *Heterotermes* comprised the overwhelming majority of termites collected in both experiments; *Coptotermes* were collected in very small numbers. Trench surveys from a related experiment estimated the average density of *Heterotermes* and of *Coptotermes* as follows: *Heterotermes*: Arid Recovery (AR) 87 ± 22 termites.m^{-2}, Scotia (SS) 137 ± 21 termites.m^{-2}, Yookamurra (YS) 112 ± 19 termites.m^{-2}. *Coptotermes*: AR 63 ± 42 termites.m^{-2}, SS 120 ± 47 termites.m^{-2}, YS 36 ± 34 termites.m^{-2}.

3.2. Experiment 1: Resource ~~consumption under increasing soil disturbance intensity and increasing aridity~~consumption.

Average resource decomposition by termites was 53.~~25~~ 3 ± 2.~~09~~ 1 % ~~upon observation~~ after 6 months' burial. We found a significant three-way interaction between the presence of digging mammals, depth and ~~aridity~~ sanctuary location (Table 3). There was no difference in resource consumption with resource depth ~~(disturbance intensity)~~ where ~~engineers~~ digging mammals were excluded (Fig. 3, post-hoc: P>0.05). However, when reintroduced ~~engineers~~ digging mammals were present, resource consumption at the low disturbance treatment (1-5 cm) was greater than at the high disturbance treatment (30-50 cm) (Fig. 3).

At 1-5 cm depths, the effect of reintroductions of digging mammals on resource consumption by termites (i.e., the difference inside and outside the sanctuary) increased with decreasing aridity (Fig. 3a-c, post-hoc: P<0.0001).

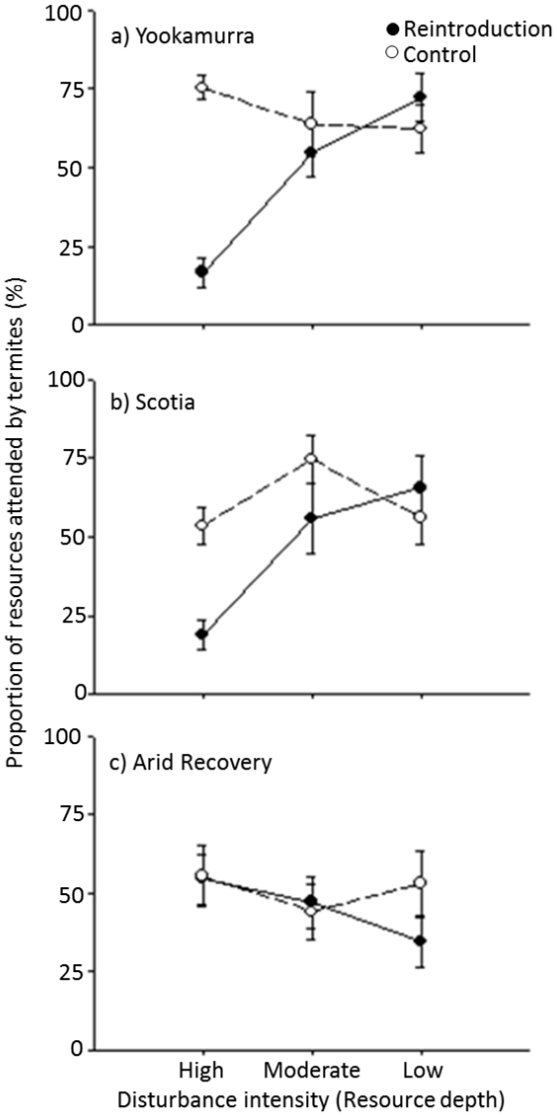

Fig. 3: Mean ± SE proportion of resources consumed by termites exposed to increasing levels of soil disturbance in Experiment I. Graphs for each sanctuary are presented in order of aridity, from least arid (a, Yookamurra), to most arid (c, Arid Recovery).

3.3. Experiment 2: Resource abandonment ~~following soil disturbance~~.

~~Soil disturbance~~Experimentally~~-~~ disturbing buried resources significantly increased ~~rates of~~ resource abandonment by termites over time~~. , and rates of~~ Resource abandonment ~~were~~ was higher when digging mammals were present (Table 4, Termites; Fig. 4a-c). ~~Aridity~~ The location of sanctuaries did not affect resource abandonment by termites (Table 4, Termites). The number of termites remaining on resources declined with time since disturbance at Yookamurra and Scotia Sanctuaries (Fig. 4a-b) (effect size contrast: 15 mins > 3 hrs > 24 hrs ($p < 0.05$). The number of termites remaining after disturbance at Arid Recovery fluctuated between the 3 hr and 24 hr observation times (Fig. 4c).

Ants were observed carrying termites away from disturbed resources and we used ant attendance at resources as a surrogate for ant predation on termites. Time since disturbance, engineer status and ~~aridity~~ sanctuary interacted to affect ant attendance at resources. Control and reintroduction sites differed after 3 hrs and 24 hrs, but only at Scotia and Yookamurra sanctuaries. At 24 hrs, the effect size (difference between control and reintroduction) decreased ~~with increasing aridity~~from Yookamurra sanctuary to Arid Recovery, which was the most arid sanctuary (Figs. 4d-f). *Iridomyrmex purpureus* was the most frequently observed ant species preying on termites.

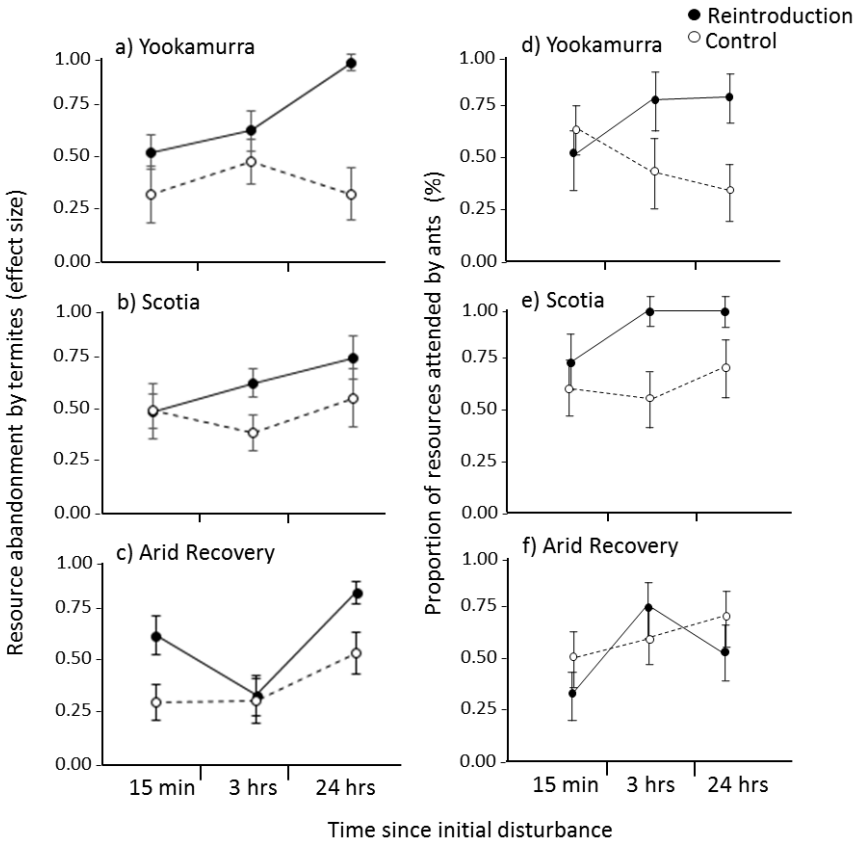

Fig. 4, Mean ± SE resource abandonment by termites (a-c) and termite predation by ants (d-f) following soil disturbance. Graphs are presented in order of the aridity at each sanctuary, from least arid (a & d, Yookamurra), to most arid (c & f, Arid Recovery).

4. Discussion

Previous studies have shown that digging mammals alter invertebrate community assemblages through ecosystem engineering (Davidson and Lightfoot, 2007; Read et al., 2008). Their effects are associated with changes to habitat structure and/or complexity, such that assemblages that take advantage of engineered habitats (for example, burrows), are distinct from surrounding habitats that have not been engineered (e.g. Bravo et al., 2009). Invertebrate ~~, and invertebrate~~ assemblages may be further altered through predation by reintroduced digging mammals and resulting trophic cascades (Silvey et al., 2015). ~~This is the first study to~~ We show that ~~interactions with digging mammals~~reintroduced digging mammals ~~also~~ negatively affect ~~ecosystem functions performed by invertebrates~~termite activity, an impact that has not been previously examined in the context of reintroducing regionally-extinct species. Termite activity was approximately 25% lower and resource abandonment about 50% higher than controls when digging mammals were reintroduced. We also observed a decrease in the effect magnitude of termite responses from Yookamurra sanctuary to Arid Recovery. These may be attributed to greater aridity levels and resource availability at Arid Recovery versus the other sanctuaries, which we will discuss.

Digging mammals such as the greater bilby and burrowing bettong move a significant volume of soil each year (Eldridge and James, 2009). Termites were expected to alter their resource consumption to avoid soil disturbances (Brown et al., 1999), resulting in ~~a decreased~~decreases ~~rate~~ of termite activity that could ultimately influence decomposition, one of their primary ecological functions. ~~-~~Data from Experiment I supported this prediction: shallow resources that were exposed to the most intense levels of soil disturbance ~~(those at shallow depths)~~ were consumed less by termites when ~~engineers~~ digging mammals were present. In contrast, resource consumption was independent of resource ~~disturbance intensity (resource depth)~~disturbance

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when ~~engineers~~ digging mammals were absent. This shift in resource consumption suggests that termites were either actively avoiding, or were less successful at consuming resources ~~where soil disturbance was greater~~ when digging mammals were present. Termite populations decline following habitat disturbances that disrupt their food supplies, for example, shortly following fires~~,~~ or when habitats shift towards lower plant diversity (e.g. in plantations) (Dosso et al., 2013). It is therefore possible that this change in function resulted from a change in population density of termites. However, preliminary data suggest that this is not the case (Coggan & Gibb in prep), so changes in resource consumption may be the result of changes in termite behaviour, considered in Experiment 2.

We showed a clear ~~(aridity dependent)~~ diminution in termite activity in the upper layers of soil in the presence of digging mammals, although this was greater at Yookamurra and Scotia sanctuaries. While previous studies have focussed on the biodiversity impacts of the loss of ecosystem engineers (Romero et al., 2015), few studies have examined the ecological cascades or functional changes resulting from changes in behaviour or population densities of species with which ecosystem engineers such as digging mammals interact. Termites are the dominant detritivores in arid Australia (Morton et al. 2011), and the change in activity resulting in lower levels of resource consumption in the presence of digging mammals may translate into decreased decomposition (in the manner that functioning decreases along disturbance intensity gradients, i.e. McDonnell et al., 1997). Any such changes in termite-driven decomposition may significantly alter soil nutrient cycling, with potential cascades through to habitat productivity. Our study suggests that reintroduction of digging mammals that function as ecosystem engineers might lead to decreases in decomposition rates, at least in the upper soil layer where foraging disturbance is most intense. Although it is possible that termite-driven decomposition has increased following the loss of digging mammals from the Australian arid zone, the outcome of

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reintroductions for nutrient cycling are likely to be complex, with further studies required to better elucidate the full complexity of interactions.

Reintroductions of digging mammals were associated with ~~increased~~ greater resource abandonment by termites, suggesting a behavioural response to disturbance might be the mechanism determining reduced resource consumption. Several species of native mammals (digging and non-digging) reintroduced to our study sites prey on invertebrates, which may result in cascading effects on invertebrate assemblages. For example, Silvey et al. (2015) documented mesopredator release in arachnid assemblages, where mammal predation reduced the abundance of the dominant scorpion species, triggering a trophic cascade in scorpion and ground-dwelling spider communities (Silvey et al., 2015). Previous studies have also reported that some species display behavioural responses to predators that minimise predation risk, but which also reduce foraging success (i.e. the 'landscape of fear', Lima and Dill, 1990), although ~~extreme~~ hunger will ~~reverse~~ alter the priorities of risk in order to avoid certain death by starvation over uncertain death by potential predators (Lima, 1998). Differences in resource abandonment ~~rates~~ between control and reintroduction sites ~~for similarly disturbed resources~~ suggest that termites may experience a landscape of fear effect in the presence of digging mammals. Laboratory experiments show that resource abandonment by termites depends on the level of danger that termites perceive (Gautam and Henderson, 2012). Increased ~~rates of~~resource abandonment in reintroductions might therefore be a result of perceived threats of predation by reintroduced native mammals (including digging species) ~~digging mammals~~ or other organisms affected by the reintroductions.

Disturbed resources were attended by ants within minutes of ~~exposure when engineers were present~~exposure, and their attendance was greater at disturbed resources when digging mammals were present. Although effects of digging mammals on ant assemblages have not been reported,

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habitat disturbance alters invertebrate assemblages, favouring aggressive ant genera such as *Iridomyrmex* (Gibb and Hochuli, 2003). Ant attendance at resources was greater in reintroduction than control sites, suggesting ant predation rates on termites may be higher when termites are exposed to disturbance when digging mammals are present. Declines in numbers of termites at resources in the presence of digging mammals may therefore have resulted from both the direct process of predation by ants or digging mammals, and the indirect process of predation or disturbance avoidance.

Changes in termite activity in the presence of digging mammals tended to be greatest at Yookamurra sanctuary, moderate at Scotia sanctuary, and not different from controls at Arid Recovery. We suggest that the differences in effect magnitude were associated with habitat (resource) availability, which differed at each sanctuary, for example, where vegetation resources covered more area at Yookamurra and Scotia than at Arid Recovery, which had more bare ground. The historical use of sanctuary land to run non-native livestock (cattle and/or sheep) before they were re-purposed for conservation is one factor that could strongly affect habitat availability. The presence of livestock in arid lands has lasting impacts on habitat structure. These include changes in the proportions of bare ground and low vegetation to taller plant types (e.g. shrubs), and the long-term impact on habitat cover can be observed when livestock is absent as those taller plant classes return (e.g. Eldridge et al., 2011). Persistent soil disturbance in addition to different mammal densities (where digging is an engineering function) also limits opportunities for plants to establish (e.g. Gurney et al., 2015; McAfee et al., 2015). Both of these factors are likely to contribute to the habitat cover observed at each sanctuary, in addition to aridity, which was lower at Yookamurra and Scotia than at Arid Recovery. The influence of rainfall (aridity) over productivity is one of the defining aspects of arid habitats (Fischer and Turner, 1978; Hadley and Szarek, 1981; Rodríguez-Castañeda, 2013), with less vegetation

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expected in more arid habitats (Oksanen et al., 1981). Results from the first experiment indicated that avoiding disturbance was important for termites in less-arid sanctuaries, where resources such as wood and leaf litter were more available. The cost of leaving a resource would be higher in more arid environments where fewer alternative resources were available. Resource scarcity, such as the low wood availability observed at Arid Recovery, might thus encourage higher fidelity to resources by termites. Different responses to resource-use based on the relative value of scarce resources have previously been observed in termites, for example, *Reticulitermes flavipes* consumed resources more slowly when resources were scarce (Lenz et al., 2009). Productivity might also affect ant predation: more productive environments might support larger densities of ants, such that the chance of discovery of termite prey would be higher. Further investigation is required to test this hypothesis.

5. Conclusions

We observed clear effects of digging mammal reintroductions on termite activity, which were significantly reduced when those mammals were present. An additional pattern suggested that termite responses were influenced by resource availability, which could be affected by factors such as aridity and land-use history. Our explicit test of termite responses to soil disturbance by mammals adds to our growing empirical understanding of interactions between digging mammals and ground-dwelling invertebrates. Our results suggest that Australian arid ecosystems may have been substantially different prior to the ecological extinction of digging mammalian engineers. They also highlight the complexity of species interactions, with mammal disturbance also altering termite interactions with invertebrate predators (ants). Termites are important food resources for other species, key detritivores in the decomposition process, and ecosystem engineers that affect soil processes and vegetation patterns, especially in arid environments (Evans et al., 2011; Gibb, 2012b; Mora et al., 2005). The lessening of termite activity when

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digging mammals were present is an interesting point to consider, as it could indicate a shift in the location of resource decomposition into deeper, less-disturbed soil. The relevance of sanctuary-specific background factors including aridity land-use history (among others) still require empirical exploration beyond what we uncovered using only three sites. The trends that we observed agree with the context-dependency of engineering impacts (McAfee et al., 2015), but run counterpoint to theories that engineering ought to benefit interacting organisms with increasing environmental adversity (Crain and Bertness, 2006). This novel finding suggests that it may be more difficult to generalise about the effects of digging mammals on ecosystems than anticipated, and that higher carrying capacities of less arid environments may also be linked with greater ecosystem sensitivity. This study adds to the small, but growing, volume of research showing that the decline of digging mammals has had broad-reaching effects on invertebrates (e.g. Davidson and Lightfoot, 2007; Silvey et al., 2015), and makes substantial advances in our understanding of impacts on invertebrate-driven decomposition, a critical ecosystem function.

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6.1. Conflict of interest disclaimer

We confirm no conflicts of interest on behalf of the authors associated with this manuscript.

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